1923

FROM

THE NEW ZEALAND

JOURNAL OF SCIENCE AND TECHNOLOGY,

VOL. VI, No. 3, p. 157–66, 1923.

Relation of Biologic Specialization in the Taxonomy of the Grass-rusts.

BY

G. H. CUNNINGHAM,

Mycologist, Biological Laboratory, Department of Agriculture, Wellington, N.Z.

WELLINGTON, N.Z.:
W. A. G. SKINNER, GOVERNMENT PRINTER
—
1923.

FROM

THE NEW ZEALAND

JOURNAL OF SCIENCE AND TECHNOLOGY,

VOL. VI, No. 3, p. 157–66, 1923.

Relation of Biologic Specialization in the Taxonomy of the Grass-rusts.

BY

G. H. CUNNINGHAM,

Mycologist, Biological Laboratory, Department of Agriculture, Wellington, N.Z.

WELLINGTON N.Z.:

W. A. G. SKINNER, GOVERNMENT PRINTER.

1923.

RELATION OF BIOLOGIC SPECIALIZATION IN THE TAXONOMY OF THE GRASS-RUSTS.‡

By G. H. Cunningham, Mycologist, Biological Laboratory, Department of Agriculture, Wellington, N.Z.

During the preparation of a recent monograph (1923) on the Uredinales of New Zealand, both of indigenous and introduced species, the writer met with considerable difficulty in determining the hosts, distribution, and specific names of many of the cereal and grass rusts. Indeed, so confusing is the literature dealing with the rusts that parasitize members of the Gramineae that the following notes have been prepared to show the complexity of the views expressed in the literature dealing with the cereal rusts, and as an attempt at their simplification. A summation

* Cunningham, G. H., *Clathrus cibarius*, or "Bird-cage Fungus," *N.Z. Jour. Sci. & Tech.*, vol. 5, p. 247, 1922.

† Carne, W. M., in Lloyd's *Mycological Notes*, vol. 7, p. 1117, 1922, Cincinnati.

‡ Read before the Australasian Association for the Advancement of Science, 16th January, 1923.

merely is given, for complete references to all the literature would extend this paper to many times its present length.

Before proceeding further it may be as well to mention that it is necessary for the taxonomist clearly to define what to his mind constitutes a species, so that some semblance of order may be preserved in any systematic paper he undertakes. From a survey of the many conflicting statements of reputable experimentalists set out below it becomes obvious that some line of defence (as it were) must be maintained by the taxonomist against the (to him) unnecessary and endless multiplication of specific names. With this end in view the writer has brought together certain evidence to justify the complaint of unnecessary name-multiplication. For, unless and until some such stand is taken, it is possible that any well-known specific name may at any moment be changed. That they are frequently being changed is obvious when the continually swelling synonymic list under each species is considered.

In this paper four only of the better-known heteroecious species are dealt with—namely, *Puccinia graminis* Pers., *P. coronata* Cda., *P. dispersa* Erikss. et Henn., and *P. Elymi* Westnd. As these species all infect cereals, and are therefore of the greatest economic importance, the literature dealing with them is extensive and complex.

HISTORICAL INTRODUCTION.

Towards the latter part of the sixteenth century it was well known to many agriculturists that the rusts on barberry (*Berberis vulgaris* L.) and wheat were in some manner connected, but no definite evidence on this point was obtained until Schoeler (1818) demonstrated the connection by actual experiment. Little credence was given to his paper by scientists of that period, however, so that the matter remained at issue until the appearance of De Bary's classical paper (1865) in which he verified the connection. De Bary first sowed teleutospores from wheat on the leaves of barberry and obtained aecidia, and in the following year carried out the converse experiment, sowing aecidiospores from barberry on the blades of wheat-seedlings and obtaining uredospores. His success led De Bary to experiment with the spores of *Puccinia coronata*, and he proved that this species also was heteroecious, the aecidium occurring on *Rhamnus Frangula*.

The publication of this paper led to work on various rusts by other experimentalists, with the result that in a few years many heteroecious species were proved to exist.

In consequence of this cultural work, workers found that certain species exhibited what is now known as biologic specialization. Little notice was taken of this phenomenon until the appearance of Eriksson's paper "On the Specialization of Parasitism of the Cereal Rusts" (1894). Although he was not the first to draw attention to this specialization, he was the first to point out that it suggested a possible method whereby "species" could be separated. This paper gave great impétus to researches in connection with specialization of parasitism in the rusts, work which has continued to the present day.

Puccinia graminis Pers.

In his paper (1894) Eriksson, as a result of numerous cultures, stated that he found teleutospores from many hosts would infect barberry, but that the aecidiospores so produced were, in their capacity for infection, limited to certain associated groups of hosts. Further experiments soon demonstrated the fact that the aecidiospores produced on barberry as a

result of infection with teleutospores taken from (say) wheat would only infect wheat; teleutospores from *Agrostis* would only infect *Agrostis;* and so on: in other words, that certain races showed definite specialization. To these races he applied the term *specialisierte Formen*, and in his paper listed several, together with the hosts to which they were confined.

In a later paper (1901) he summarized this experimental work, as under:—

1. *Puccinia graminis* Pers. Aecidium on *Berberis vulgaris.*
   1. f. *Secalis.* On rye.
   2. f. *Avenae.* On oat.
   3. f. *Tritici.* On wheat.
   4. f. *Airae.* On *Aira caespitosa.*
   5. f. *Agrostidis.* On *Agrostis* spp.
   6. f. *Poae.* On *Poa* spp.
2. *Puccinia Phlei-pratensis* Erikss. et Henn. Aecidium unknown. On timothy. (This latter species was separated by Eriksson and Henning (1894, p. 140) on account of inability of the teleutospores to infect barberry.)

Eriksson insisted on the rigid specialization of these races, but results obtained by subsequent workers do not bear this out. For example, Carleton (1899), working with practically the same races, obtained quite different results. He claimed that in North America there were only two special forms (races) as under:—

1. f. *Tritici.* On wheat, barley, cocksfoot, *Agrostis alba, Festuca gigantea, Koeleria cristata,* and *Hordeum murinum.*
2. f. *Avenae.* On oat, cocksfoot, *Avena fatua, A. pratensis, Hordeum murinum, Koeleria cristata, Holcus mollis,* &c.

Jaczewski (1910), working in Russia with similar material, obtained results that showed he was working with five biological races, equivalent to—1, f. *Secalis;* 2, f. *Tritici;* 3, f. *Avenae;* 4, f. *Hordei;* 5, f. *Agrostidis.*

Stakman and Piemeisel (1917), working with this species from both cereals and grasses, separated, as a result of numerous cultures, the following six biological races: 1, f. *Tritici;* 2, f. *Tritici-compacti;* 3, f. *Secalis;* 4, f. *Avenae;* 5, f. *Phlei-pratensis;* 6, f. *Agrostidis.* They claim (*l.c.*, p. 484) that, although the uredospores of these races are similar in size and shape, yet if large numbers are measured, and the biometrical mode determined, appreciable and fairly constant differences become apparent, *provided the spores measured be taken from cogenial hosts.* [The italics are ours.] They state, moreover, that "more than one biologic form (race) may occur on the same host in nature, sometimes even on the same plant."

In a recent paper (1922) Stakman and Levine record the discovery of some thirty-seven biological races on wheat. *Puccinia Phlei-pratensis* Erikss. et Henn. is by Stakman and Piemeisel included as a biological race of *P. graminis,* and not considered as a distinct species. This has been done as the result of cultural work recorded in two previous papers (Stakman and Jensen, 1915; Stakman and Piemeisel, 1916). In the former paper the authors claimed that by direct transference of uredospores from timothy they were able to infect several cereals and grasses, thus showing that this race is not limited to the one host, as Eriksson claimed.

As much of the experimental work discussed above has been carried out with uredospores, it might be supposed that different results would be obtained if the cultures were performed with aecidiospores and teleutospores, especially as the aecidium has, by several authors, been considered either the result of a sexual process (Massee, 1888; Blackman, 1904) or a device to reinvigorate the organism (Arthur, 1903; Bolley and Prichard, 1906).

Eriksson (1896), after numerous experiments, claimed that the aecidium did not influence the biologic races dealt with to the extent of causing them to become more vigorous or widespread in infective capabilities. This statement is supported by Stakman, Piemeisel, and Levine (1918), who, after cultural work extending over four seasons, came to the conclusion that "barberry does not increase the host range of biologic forms, nor does it act as a reinvigorator of the rust. The biologic specialization in the aecial stage is apparently the same as that in the uredinial stage." Arthur (1920, p. 228), on the other hand, claims that the aecidium exerts a reinvigorating influence, for he states, "More extended work is planned in regard to the problem of the transfer of this pernicious black or stem rust from wild grasses to the cultivated cereals, but enough has been accomplished to warrant the statement that although in the uredinial stage this rust shows racial strains that inhibit the ready transfer from one species to another, yet in the aecial stage racial strains play no part, and the barberry acts as a bridging host between each and every other gramineous host."

Puccinia coronata Cda.

Corda (1837) applied to a species of *Puccinia* characterized by the coronate apex of the teleutospore the specific name *coronata*. Nielsen (1875) showed that when aecidiospores from *Rhamnus cathartica* were sown on leaves of *Lolium perenne* uredospores appeared, whereas when aecidiospores from *Rhamnus Frangula* were used no infection resulted. Consequently he considered the former race to be sufficiently distinct to be considered as a separate species, which he named *Puccinia Lolii*. Seventeen years later Klebahn (1894, p. 135) sowed teleutospores from *Lolium perenne* on *Rhamnus Frangula* and *R. cathartica* respectively, and, as he obtained infection on the latter host, he proposed separating this race as a distinct species, for which he suggested the name *P. coronifera*, apparently overlooking the fact that it had previously been isolated and named by Nielsen. He also verified the connection between the aecidium on *Rhamnus Frangula* and *Puccinia coronata*. In passing, it may be mentioned that the aecidia of these two races are morphologically identical.

Eriksson (1894) divided each of these so-called species into five races. In a later paper (1908) he revised his previous work and split *P. Lolii* into eight races, allowing *P. coronata* to remain as in his previous paper. Carelton (1899), on the other hand, claimed that there is but one host of *P. Lolii* in nature. As these races have not been considered as being specifically distinct, it is not necessary to detail them here.

Puccinia dispersa Erikss. et Henn.

This species was at first included in the aggregate *P. rubigo-vera* Wint., but was separated by Eriksson and Henning (1894), together with *P. glumarum* Erikss. et Henn. and *P. simplex* Erikss. et Henn., on account of certain morphological differences, principally in the uredosori. The same year (1894) Eriksson claimed that *P. glumarum* and *P. dispersa* each consisted of five

biological races. In a later work (1899) he revised his previous work and divided the original *P. rubigo-vera* into the following species :—

1. *Puccinia glumarum* Erikss. et Henn. Aecidium unknown.
2. *Puccinia dispersa* Erikss. Aecidium on *Anchusa* sp.
   Grove (1913, p. 261) stated that if this specific name were retained confusion would follow, as it had previously been used by Eriksson and Henning; he therefore proposed to name this race *P. secalina* Grove.
3. *Puccinia triticina* Erikss. Aecidium unknown. (Since shown to occur on *Thalictrum* spp.)
4. *Puccinia bromina* Erikss. Aecidium unknown.
   F. Mueller (1901) found by the aid of cultures that the aecidium of this race occurred on *Symphytum officinale* L., and accordingly named it *P. Symphyi-bromorum* F. Meull.
5. *Puccinia agropyrina* Erikss. Aecidium unknown.
6. *Puccinia holcina* Erikss. Aecidium unknown.
7. *Puccinia Triseti* Erikss. Aecidium unknown.
8. *Puccinia simplex* Erikss. et Henn. Aecidium unknown. (Now known to occur on *Ornithogalum* sp.)

Of these, Arthur and Fromme (1920) recognize Nos. 1, 2, 6, and 8 (as *Dicaeoma glumarum* Arth. and Fromme, *D. Asperifolii* Kuntze, *D. holcinum* Arth. and Fromme, and *D. anomalum* Arth. and Fromme). *Puccinia triticina* Erikss. and *P. agropyrina* Erikss. they include as synonyms under *Dicaeoma Clematidis* Arth. (= *P. Elymi* Westnd.).

Puccinia Elymi Westnd. (1851).

The uredo- and teleuto-spores of this species occur on several species and genera of the Gramineae, the aecidia on several species and genera of the Ranunculaceae, and because of these numerous hosts many races have been described as distinct species.

For example, Plowright (1885), through cultures, found that an aecidium on *Ranunculus acris* was the first stage in the cycle of a *Puccinia* on *Alopecurus pratensis;* this race he named as *Puccinia perplexans* Plowr.

Three years later (1889) he sowed teleutospores from *Agropyron repens* on *Thalictrum flavum* and obtained aecidia; he carried out the converse experiment and obtained uredospores; consequently he decided that he was working with an undescribed species, to which he gave the name *Puccinia persistens* Plowr.

Later (1890) he worked out by the aid of cultures the connection between an aecidium on *Aquilegia vulgaris* and a *Puccinia* on *Agrostis alba* and *A. vulgaris;* as a result he erected the species *Puccinia Agrostidis* Plowr.

Ellis and Everhart (1892) described as new a species of *Puccinia* on *Agropyron* spp.—*Puccinia Agropyri* Ell. et Ev. Dietel (1892) infected leaves of *Clematis vitalba* with teleutospores of this species from *Agropyron glaucum*, and, as a result, concluded that this aecidium was a stage in the cycle of *P. Agropyri* Ell. et Ev.

Juel (1894) connected by cultures an aecidium on *Thalictrum alpinum* with a *Puccinia* on *Agrostis* sp. and *Anthoxanthum* sp.: to this he gave the name *P. borealis* Juel.

Rostrup (1898), with aecidiospores from *Thalictrum minus*, succeeded in infecting *Elymus arenarius*, and, as a result, considered this accidium to be a stage in the cycle of *P. Elymi* Westnd.

Eriksson (1899), on account of their biologic specialization, separated as distinct species *P. triticina* Erikss. and *P. agropyrina* Erikss. from the collective species *P. rubigo-vera* Wint. These were subsequently placed by Arthur and Fromme (1920) under *Dicaeoma Clematidis* Arth., a procedure in part confirmed by the later work of Jackson and Mains (1921).

Ed. Fischer (1901) connected an aecidium on *Actaea* with teleutospores of a species of *Puccinia* on *Agropyron* sp.: to this he gave the name *P. Actaeae-Agropyri* Ed. Fisch.

Arthur (1909), by the aid of cultures, connected an aecidium on *Thalictrum dioicum* with teleutospores of a *Puccinia* on *Bromus Porteri:* this he named *P. alternans* Arth. The following year (1910) he recorded successful inoculations of *Aquilegia canadensis* with teleutospores of a *Puccinia* from *Agropyron biflorum:* this he named *P. obliterata* Arth.

E. Mayor (1911) connected an aecidium on *Actaea spicata* with uredo- and teleuto-spores on *Elymus europaeus:* to this race he gave the name *P. Actaeae-Elymi* E. Mayor.

Jackson and Mains (1921) discovered that the hitherto unknown aecidium of "*Puccinia triticina* Erikss." occurred on several species of *Thalictrum*. They consider that, on account of the morphology and host relationships, this species is "closely related to *Puccinia persistens, P. borealis, P. alternans, P. obliterata, P. Elymi*, and *P. Agropyri*, but is separable from these rusts by its sharp biologic limitation to wheat." This largely confirms the work of Arthur and Fromme (1920, p. 333), who include all these races, on account of their morphological similarity, under *Dicaeoma Clematidis* Arth. As their name cannot hold under the International Rules of Botanical Nomenclature, so the species must be called *Puccinia Elymi* Westnd., as this was the first name applied to the perfect stage when placed in the correct genus.

CONCLUSION.

From a consideration of the statements set out above it becomes obvious that the earlier workers considered all races showing biologic specialization of sufficient importance to raise to specific rank, regardless of the absence of morphological differences. It becomes equally clear that the modern tendency is to limit species to those possessing morphological differences, and to group under one species all races resembling one another, regardless of the fact that they may differ greatly in their biologic specialization. In other words, to-day biologic specialization alone is not considered a specific character. As to whether the presence or absence of an aecidium should be considered a character sufficient to warrant the separation of a species is a matter that would to a great extent depend on the evidence brought forward in support. For instance, if it is claimed that the aecidium is absent from the cycle of a certain species, and this claim is made merely on negative cultures (negative evidence), the writer believes that this cannot be accepted as evidence upon which to separate a species. On the other hand, if failure to produce aecidia by the aid of cultures is supported by evidence as to the presence of spermogones associated with the uredosori or teleutosori, then results may be capable of a different interpretation. Similarly, if the aecidia upon different hosts resemble one another morphologically, and if they have been connected by cultures with teleutospores also resembling one another, the fact that they each exhibit definite

and clear-cut specialization does not indicate that they are separate species; they should be classed as races of the same species.

For example, Eriksson and Henning separated *P. Phlei-pratensis* from *P. graminis*, the reason given being that teleutospores from hosts of *P. graminis* would infect barberry, whilst those from timothy (the host of their *P. Phlei-pratensis*) were incapable of doing so. Stakman and Piemeisel, whilst admitting they could not infect barberry with teleutospores from timothy, showed by numerous cultures that the uredospores of this race were quite capable of producing uredospores on numerous cereals and grasses, hosts of several races of *P. graminis*, and that the resultant spores were identical with uredospores of other races of *P. graminis*. Therefore they concluded that *P. Phlei-pratensis* was but a biological race of *P. graminis*. If the absence of an aecidium in this case is considered sufficient to separate a species, then the form of *P. graminis* occurring in New Zealand, Australia, and South Africa must be considered as specifically distinct from the European form, for although it is common on many introduced and indigenous cereals and grasses, yet in no single instance in any of these countries has the aecidium been obtained on barberry, either in nature or from cultures.*

The synonymy of this species then is :—

Puccinia graminis Pers.

1. *Puccinia Phlei-pratensis* Erikss. et Henn.

Puccinia coronata Cda.—This is usually split into two species on account of the biologic specialization exhibited by the aecidia. As the writer believes that only one morphological species exists in nature, he would arrange the synonymy as under :—

Puccinia coronata Cda.

1. *Puccinia Lolii* Niels.
   Puccinia coronifera Kleb.

Puccinia dispersa Erikss. et Henn., it will be remembered, was derived from the collective *P. rubigo-vera* Wint. Then Eriksson split *P. rubigo-vera* into eight species, most of which are based on biologic grounds only, and consequently cannot be recognized. Therefore the synonymy is as follows :—

Puccinia dispersa Erikss. et Henn.

1. *Puccinia dispersa* Erikss.
   P. secalina Grove.
2. *Puccinia triticina* Erikss.
3. *Puccinia bromina* Erikss.
   P. Symphyti-bromorum F. Muell.
4. *Puccinia agropyrina* Erikss.
5. *Puccinia Triseti* Erikss.

In reality Nos. 2 and 4 are synonyms of the following species, but are retained here to show their derivation.

* Since the above was written the writer has seen a paper by Waterhouse (*Proc. Roy. Soc. N.S.W.*, vol. 55, pp. 278–88, 1922) in which he records successful innoculation of barberry with teleutospores collected from wheat-plants grown in Australia. Although the results were obtained under highly artificial conditions, his experiments show that one at least of the Australian biological races are still capable of producing aecidia.

Puccinia Elymi Westnd. has been split into many so-called species on account of the fact that the aecidia of different races occur on many different hosts. Later work has shown that these races do not exhibit even biologic distinctions; consequently the synonymy is as under:—

Puccinia Elymi Westnd.

1. *P. perplexans* Plowr.
2. *P. persistens* Plowr.
3. *P. Agrostidis* Plowr.
4. *P. Agropyri* Ell. et Ev.
5. *P. borealis* Juel.
6. *P. Actaeae-Agropyri* Ed. Fisch.
7. *P. Actaeae-Elymi* E. Mayor.
8. *P. alternans* Arth.
9. *P. obliterata* Arth.
   (*P. agropyrina* Erikss.).
   (*P. triticina* Erikss.).

Many other examples could be cited, but the examples chosen will illustrate the complexity of modern taxonomy. Although only four species are discussed in this paper, yet nineteen synonyms are listed, all the outcome of so-called species based on biologic distinctions alone. This by no means includes all, as there are forty-five for *P. Elmyi* alone; but as thirty-four of these are not due to cultural work they have been omitted here.

When it is considered that few workers have obtained similar results when working with similar material, and that a great deal of the evidence submitted in support of the erection of species is negative evidence, it becomes obvious that the taxonomist can place little reliance upon cultural work as a basis for specific determination, and this fact would appear to strengthen the contention of Marshall Ward (1905) that "no species can be accepted as valid until it is capable of definition in morphological terms."

In conclusion the writer would like to state that he does not wish to disparage cultural work—far from it; as an economic mycologist he fully realizes the debt mycologists and plant pathologists owe to those workers who have engaged in this exacting research, particularly to those who have devoted so much time to the problem of cereal rusts, their biology, distribution, and possible control. At the same time he believes that, from the taxonomist's point of view, this work must of necessity be given little credence, partly because the taxonomist so frequently has to work with herbarium material, but principally because there is the danger that unless some such stand is taken we may in the future be confronted by some publication based on the lines laid down by Probst (1909), who claimed that a certain species of *Puccinia* was confined to a single form of a variety of a species of the host genus *Hieracium*. Carry this to its ultimate conclusion and systematic work would become unnecessary, as each rust on each individual plant could be considered as a distinct species, and named accordingly.

LITERATURE CITED.

ARTHUR, J. C., 1903. The Aecidium as a Device to restore Vigour to the Fungus, *Proc. Prom. Agr. Sci.*, vol. 23.

—— 1909. Cultures of Uredineae in 1908, *Mycologia*, vol. 1, p. 248.

—— 1910. Cultures of Uredineae in 1909, *ibid.*, vol. 2, p. 228.

ARTHUR, J. C., and FROMME, F. D., 1920. Dicaeoma on Poaceae, *North American Flora*, vol. 7, pp. 277–341.

BARY, A. de, 1865. Neue Untersuchungen ueber Uredineen, pt. 1, *Monatsber. K. Preuss. Akad. Wiss.*, Berlin, p. 15.

BLACKMAN, V. H., 1904. On the Fertilization, Alternation of Generations, and General Cytology of the Uredineae, *New Phytologist*, vol. 3, p. 23.

BOLLEY, H. L., and PRICHARD, F. J., 1906. Rust Problems: Facts, Observations, and Theories; Possible Means of Control, *N. Dak. Agr. Exp. Stn. Bull. 68.*

CARLETON, M. A., 1899. Cereal Rusts of the United States: A Physiological Investigation, *U.S. Dept. Agr., Div. Veg. Physiol. and Path., Bull. 16*, pp. 1–74.

CORDA, A. C. J., 1837. *Icones Fungorum hucusque cognitorum*, vol. 1, pp. 1–32.

CUNNINGHAM, G. H., 1923. The Uredinales or Rust Fungi, of New Zealand, pt. 1, Pucciniaceae, *Trans. N.Z. Inst.*, vol. 54, pp. 619–704.

DIETEL, P., 1892. Ueber den Generationswechsel von Puccinia Agropyri, *Oesterr. Bot. Zeitschr.*, vol. 42, p. 261.

ELLIS, J. B., and EVERHART, B. M., 1892. New Species of Fungi, *Jour. Myc.*, vol. 7, p. 130.

ERIKSSON, J., 1894. Ueber die Spezialisierung der Parasitismus bei den Getreiderospilzen, *Ber. Deut. Bot. Gesell.*, Band 12, Heft 9, p. 292.

—— 1896. Welche Grasarten koennen die Berberitze mit Rost anstecken? *Zeitschr. Pflanzenkr.*, Band 6, Heft 4, p. 193.

—— 1899. Nouvelles Etudes sur la Rouille Brune des Cereales, *Ann. Sci. Nat.*, ser. 8, vol. 9, p. 241.

—— 1901. Sur l'Origine et la Propagation de la Rouille des Cereales par la Semence, *ibid.*, vol. 14, pp. 1–124.

—— 1908. Neue Studien ueber die Spezialisierung der Grasbewohnenden Kronenrostarten, *Arkiv. foer Botanik*, vol. 8, no. 3, p. 126.

ERIKSSON, J., and HENNING, E., 1894. Die Hauptresultate einer neuen Untersuchung ueber die Getreideroste, *Zeitschr. Pflanzenkr.*, Band 4, pp. 66, 140, 192, 257.

FISCHER, E., 1901. Fortsetzung der Entwicklungsgeschichtlichen Untersuchungen ueber Rostpilze, *Ber. d. Schweiz. Bot. Gesellsch.*, vol. 11, pp. 1–14.

GROVE, W. B., 1913. *The British Rust Fungi.* Cambridge.

JACKSON, H. S., and MAINS, E. B., 1921. Aecial Stage of the Orange Leaf-rust of Wheat, Puccinia triticina Erikss., *Jour. Agr. Res.*, vol. 22, pp. 151–72.

JACZEWSKI, A. DE, 1910. Studien ueber das Verhalten des Schwarzrostes des Getreides in Russland, *Zeitschr. Pflanzenkr.*, Band 20, Heft 6, pp. 321–59.

JUEL, H. O., 1894. Mykologische Beitraege, 1, Zur Kenntniss Einiger Uredineen aus den Gebirgsgegenden Skandinaviens, *Oefvers. K. Svenska. Ventensk. Akad. Foerhandl.*, arr. 51, no. 8.

KLEBAHN, H., 1894. Kulturversuche mit Heteroecischen Uredineen, *Zeitschr. Pflanzenkr.*, vol. 4, pp. 7, 84, 129, 135.

MASSEE, G., 1888. On the Presence of Sexual Organs in Aecidium, *Ann. Bot.*, vol. 2, p. 47.

MAYOR, E., 1911. Recherches Experimentales sur quelques Uredinees Heteroiques, *Ann. Mycol.*, vol. 9, no. 4, pp. 358–62.

MUELLER, FRITZ, 1901. Beitraege zur Kenntniss der Grasroste, *Bot. Centbl. Beihefte*, Band 10, Heft 4, 5, pp. 181–212.

NIELSEN, P., 1875. De for Landbruget Farligst: Rustarter og Midlere imad den, *Ugeskr. for Landmaend.*, vol. 4, no. 9, pp. 549–56.

PLOWRIGHT, C. B., 1885. On the Life-history of certain British Heteroecismal Uredines, *Quart. Jour. Micr. Sci.*, vol. 25, pp. 164–66.

—— 1889. *A Monograph of the British Uredineae and Ustilagineae*, p. 181. London.

—— 1890. British Uredineae, *Gard. Chron.*, ser. 3, vol. 8, p. 139.

PROBST, RENE, 1909. Die Spezialisation der Puccinia Hieracii, *Centbl. f. Bakter*, pt. 2, vol. 22, pp. 675–720.

ROSTRUP, F. G. E., 1898. Et nyt Vaertskifte hos Uredinaceerne og Konidier hos Thecaphora Convolvuli, *Oversigt. K. Danske Vidensk. Salsk. Fordhandl.*, no. 5, pp. 269–76.

SCHOELER, O., 1818. Berberissens Skadelige Indflydelse, isaer paa Rugen, *Landaekomminske Tidender*, pt. 8, p. 289.

STAKMAN, E. C., and JENSEN, L., 1915. Infection Experiments with Timothy-rust, *Jour. Agr. Sci.*, vol. 5, pp. 211–16.

STAKMAN, E. C., and PIEMEISEL, F. J., 1916. Infection of Timothy by Puccinia graminis, *ibid.*, vol. 6, pp. 813–16.

STAKMAN, E. C., and PIEMEISEL, F. J., 1917. Biologic Forms of Puccinia graminis on Cereals and Grasses, *ibid.*, vol. 10, pp. 429–95.

STAKMAN, E. C., PIEMEISEL, F. J., and LEVINE, M. N., 1918. Plasticity of Biologic Forms of Puccinia graminis, *ibid.*, vol. 15, pp. 221–49.

STAKMAN, E. C., and LEVINE, M. N., 1922. The Determination of Biologic Forms of Puccinia graminis on Triticum spp., *Univ. Minnesota Agr. Exp. Stn. Bull. 8*, pp. 1–8.

WARD, H. MARSHALL, 1905. Recent Researches on the Parasitism of Fungi, *Ann. Bot.*, vol. 19, pp. 1–54.

WESTENDORP, G. D., 1851. Sur quelques Cryptogams Inedites or Nouvelles pour la Flore Belge, *Bull. Acad. Sci. Brux.*, vol. 18, pt. 2, p. 408.

[100/11/23—16360